

Cover Page

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Long-term Memory of Past Events in Great Apes

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Abstract

It has been claimed that the ability to recall personal past events is uniquely human. We review recent evidence that great apes can remember specific events for long periods of time spanning months and even years, that such memories can be enhanced by distinctiveness (irrespective of reinforcement), and follow a forgetting curve similar to humans. Moreover, recall is enhanced when apes are presented with features that are diagnostic of the event, consistent with notions of encoding specificity and cue-overload in human memory. These findings are consistent with the involuntary retrieval of past events in humans, a mode of remembering that is thought to be less cognitively demanding than voluntary retrieval. Taken together, these findings reveal further similarities between the way humans and animals remember past events and open new avenues of research on long-term memory in non-human animals.

Keywords: Great Apes, Long-term Memory, Spontaneous Retrieval, Episodic Memory, Event Memory.

Long-term Memory of Past Events in Great Apes

“The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind.” (Darwin, 1874, p. 126).

Great apes have remarkable memories. They can recall information and skills learnt many years previously, such as the meanings of lexigrams (Beran & Heimbauer, 2015), abstract concepts (Patterson & Tzeng, 1979) and tool construction techniques (Vale et al., 2016). For the last two decades there has been great interest in whether they (and other animals) also remember specific events from their past. We review what is currently known about great apes’ memory for past events (for reviews in other species, see recommended readings). We begin with early work that focused on the recall of ‘what’, ‘where’ and ‘when’ information from a past event, referred to as episodic-like memory (Clayton & Dickinson, 1998), before turning to recent novel paradigms that show similarities with human involuntary episodic memory.

Episodic-like Memory in Apes

Episodic memory is memory for personally experienced past events (Tulving, 1972). It involves the subjective experience of mentally travelling back in time (autonoetic consciousness), and a self-awareness of one’s past, future and present (chronesthesia) (Tulving, 2001). Demonstrating conscious experience in populations without language is extremely challenging, and as of yet, there is no standard agreement upon non-linguistic markers of conscious recollection. As such, episodic memory in animals has conventionally been investigated using criteria based on content; that is, the recall of ‘what’, ‘where’ and ‘when’ (w-w-w) from a single episode. Clayton and Dickinson (1998) termed this episodic-like memory, in acknowledgement of the lack of measures of conscious awareness.

One of the first demonstrations of chimpanzee memory for ‘what’ and ‘where’ was provided by Tinklepaugh (1932). He presented two chimpanzees with two containers and hid food (e.g., banana)

under one of them. Before the chimpanzees could make a choice, a screen was positioned over the two containers and the hidden banana was substituted with a different type of food (e.g., orange). The chimpanzees successfully selected the container under which they had seen banana being hidden, but hesitated when they saw that an orange was there. This behaviour suggests that they not only remembered where the food was hidden, but also what had been hidden, as the hesitant behaviour was observed only when the food was substituted. Similarly, a chimpanzee spontaneously communicated to a person (using lexigrams, gestures, gazing and vocalisations) about what food had been hidden and where, up to sixteen hours after she witnessed the foods being hidden (Menzel, 1999). Indeed, there are numerous other examples of apes' memory for 'what' and 'where' (see Scheumann & Call, 2006; Schwartz & Evans, 2001).

Regarding memory for 'when', Schwartz, Hoffman, and Evans (2005) showed that a gorilla, King, could remember what he had eaten and in what order. King was given three different foods, one at a time. After a delay, he correctly selected cards that depicted the foods he had eaten and in the (reverse) order in which he had eaten them, suggesting he remembered the order of events. Martin-Ordas, Haun, Colmenares, and Call (2010) tested apes using a paradigm developed from Clayton and Dickinson's (1998) test of episodic-like memory in scrub jays. Apes needed to remember under which container ('where') frozen juice ('what') had been hidden. However, in order to obtain the frozen juice before it had melted, they needed to recall whether it was hidden five minutes or one hour ago ('when'). Demonstrating memory of all three w-w-w components, the apes successfully chose the container where the frozen juice was hidden after the short delay, and switched to the container in which less preferred, but edible, raisins had been hidden after the long delay (but see, Dekleva, Dufour, de Vries, Spruijt, & Sterck, 2011).

Other research has investigated 'what-who' combinations. Because human episodic memory often contains more details than 'what' was 'where' and 'when', investigating the memory of other parts is important. For instance, King (the gorilla) could remember what he had eaten and who had given him the food, after a delay of 24 hours (Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002). However, a recent study by Lewis, Berntsen, and Call (2018) suggests that the 'who' information must

be salient to be successfully remembered, with apes failing to encode/remember ‘who’ rewarded ‘what’, probably because the person was not a salient feature in the paradigm. This highlights the importance of carefully interpreting results in animal research where subjects receive no instructions regarding what to attend to, and future research should clarify that a failure to remember is not just a failure to attend.

Despite numerous examples of apes’ memory for elements of past events, the criteria deemed as necessary to show episodic-like memory has changed substantially from Clayton and Dickinson’s (1998) original definition, to include incidental encoding (Zentall, Clement, Bhatt, & Allen, 2001), binding and flexibility (Clayton, Yu, & Dickinson, 2003), amongst others. Consequently, the criteria used in different studies have become more variable and the connection to underlying memory concepts less consistent across studies and with the literature on human memory. We therefore review an alternative approach that draws upon recent developments in the conceptualization of human memory for past events (Rubin & Umanath, 2015) and research on involuntary episodic memories in humans (Berntsen, 2009; Berntsen, 2010).

Involuntary Episodic Memories

Involuntary episodic memories are memories of personal past events that are brought to mind spontaneously, without immediately preceding attempts at retrieval (Berntsen, 1996). They are well established in human autobiographical memory and provide an alternative approach to the study of past events in non-human animals. Involuntary memories often occur when features in the current environment overlap with features of the remembered event (Berntsen, Staugaard, & Sorensen, 2013). When this overlap is diagnostic of a specific event, the event is likely to be spontaneously remembered, consistent with the notion of encoding specificity (Tulving & Thomson, 1973), cue-overload (Watkins & Watkins, 1975) and cue-distinctiveness (Hunt & Smith, 1996). There are numerous ways in which a cue(s) can successfully isolate a specific memory (Berntsen, 2009). Here we present three examples (they should be seen as examples and not as an exhaustive account). For instance, a single cue can trigger a memory if it is unique to one memory (i.e., it is not overloaded;

Figure 1, Cue environment 1). Even if the cues taken individually are relevant to multiple memories, a combination of cues can create a unique constellation that is specific to one memory (Figure 1, Cue environment 2). Cues that are not unique to one memory (even when combined) can also result in successful retrieval of a specific event, if one of the memories that the cue matches is distinctive from all other memories (Figure 1, Cue environment 3; Hunt & Worthen, 2006).

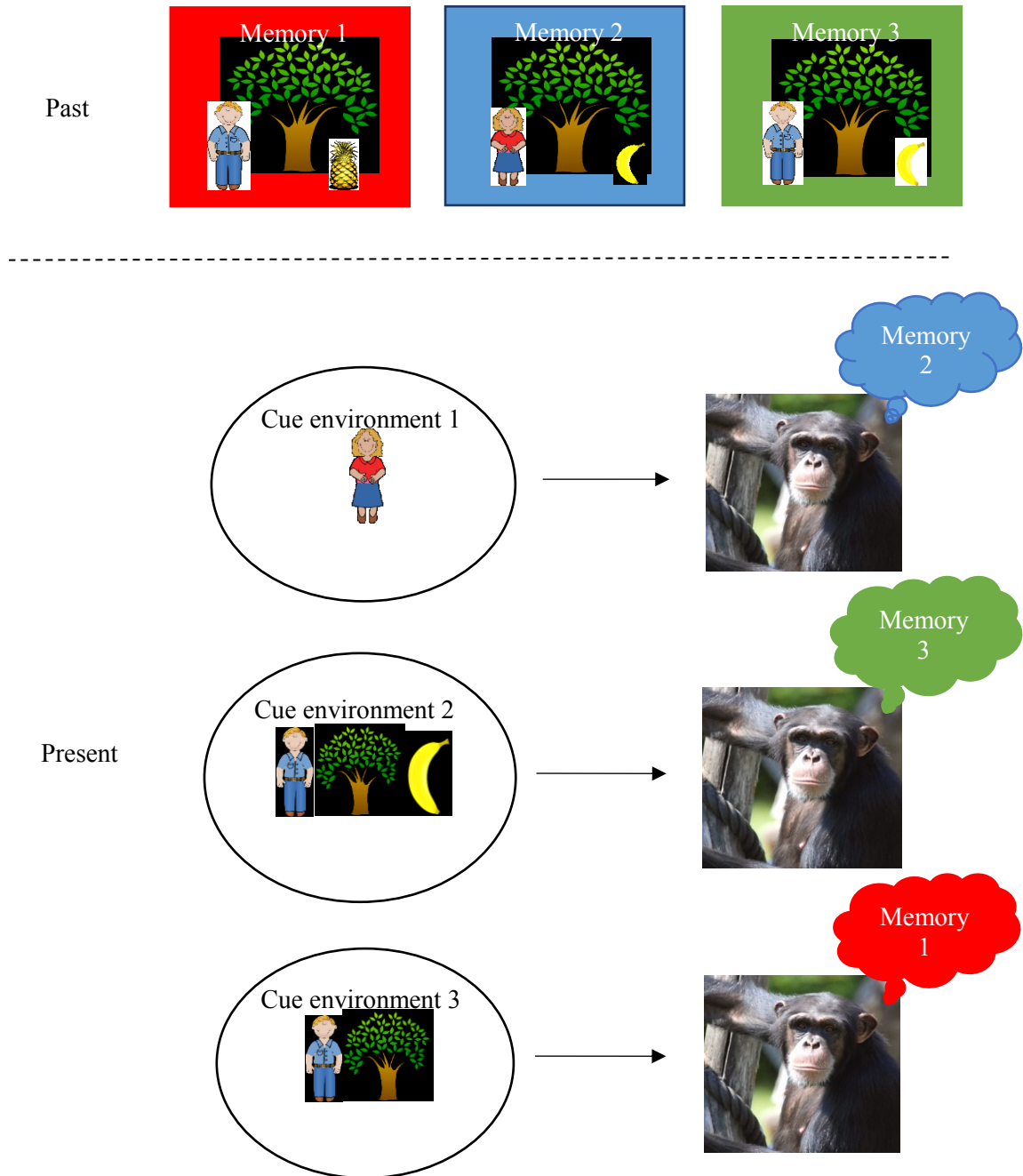


Figure 1. An illustration of spontaneous memory retrieval as a result of diagnostic cueing and event distinctiveness. In Cue environment 1, the cue is unique to Memory 2 and thus Memory 2 is retrieved. In Cue environment 2, none of the cues are unique to a single memory, but the combination of cues is unique to Memory 3 resulting in retrieval of Memory 3. In Cue environment 3, the cues in isolation are not unique to a single memory, and when combined match both Memory 1 and 3. However, because the event in Memory 1 is distinctive due to the novel pineapple feature, this memory is likely to be retrieved. Photo used with permission from the Max Planck Institute for Evolutionary Anthropology.

Involuntary memories are less cognitively demanding than voluntary memories. This is supported by studies showing shorter retrieval times for involuntary than for voluntary memories in behavioural experiments (e.g., Berntsen et al., 2013; Schlagman & Kvavilashvili, 2008). Furthermore, a brain imaging study showed that, compared with involuntary memories, voluntary memories of scenes elicited greater activity in dorsal frontal regions, typically associated with retrieval effort, whereas areas typically associated with successful episodic recollection were similarly engaged by both types of memories (Hall et al., 2014). Thus, the two types of retrieval appear to sample from the same underlying memory structures, but through different retrieval routes, with the involuntary route being less effortful. This is consistent with research showing that young children can spontaneously recall a past event when presented with distinct overlapping cues, but have difficulty intentionally retrieving a past event (Krojgaard, Kingo, Jensen, & Berntsen, 2017).

Consequently, it has been proposed that animals may also have the involuntary mode of remembering (Berntsen, 2009). Below we present recent research with apes that is consistent with this proposal. Specifically, the research shows successful retrieval of specific past events as a result of diagnostic cueing and distinctiveness, irrespective of reinforcement. These findings complement research with chimpanzees showing the use of gesturing, vocalisation and symbols as a means to communicate about past events (Menzel, 1999), and are consistent with recent findings that rats can mentally replay a stream of unique past events (Panoz-Brown et al., 2018).

Spontaneous Memories in Apes

Apes can remember details from past events when presented with cues that provide a diagnostic overlap with the remembered event (Figure 1, Cue environments 1 and 2). For instance, Kano and Hirata (2015) presented chimpanzees with a film in which a ‘King Kong’ character entered through one of two doors and attacked a human. Whilst watching the film, an eye-tracker monitored the ape’s gaze. Twenty-four hours later, the apes watched the film again and made anticipatory looks towards the door in which ‘King Kong’ had previously entered; that is, they looked at the door before the character entered, suggesting that they recalled what happened next. The apes received food

regardless of their looking behaviour and only saw the film once, thus associative learning through reinforcement is unlikely. In a second film, an experimenter selected one of two items and attacked 'King Kong'. The apes made anticipatory looks towards the item that was selected, even when the items locations were switched from the original viewing. Thus, the apes demonstrated memory of 'where' and 'what', when cued with preceding parts of the film (see also Mendes & Call, 2014).

Examining distinctiveness (Hunt & Worthen, 2006; Hunt & Smith, 1996), Lewis, Call, and Berntsen (2017a) demonstrated that apes can remember a distinctive event when probed by features that overlap with the distinctive event (Figure 1, Cue environment 3). Apes remembered which container food had previously been hidden under when presented with cues that occurred during the hiding event, but only when the event was distinctive. When the hiding event occurred in a location experienced daily, with familiar apparatus, experimenters and baiting procedure, the apes failed to remember the location of the hidden food. However, when the hiding event was made distinctive, by increasing the amount of food and by using a novel baiting procedure, the apes successfully remembered the location. Moreover, a third experiment showed that performance was not explained by reinforcement. Apes in a reinforced condition received banana during the hiding event, whereas apes in a non-reinforced condition received no food, and instead saw a distinctive act of banana being 'thrown away'. The apes in the reinforced condition failed to remember the location of the banana, whereas the apes in the non-reinforced, but distinctive, event condition successfully remembered this (Figure 2; see also Beran, 2011 for a distinctiveness effect in recognition memory in a study with chimpanzees).



Figure 2. Percentage of apes that chose the correct location by condition. A correct choice was the container that had previously been baited with food. As there were three containers, chance was 33%. (* $p < 0.05$) (Adapted from Lewis et al., 2017a).

Apes can also remember past events after very long delays. For instance, apes remembered a tool hiding event that occurred three years ago when presented with the same tool task, experimenter and location as during the initial hiding event (Martin-Ordas, Berntsen, and Call, 2013). Likewise, a recent study by Lewis, Call, and Berntsen (2017b) found that apes remembered a specific hiding event after a delay of up to 50 weeks, when presented with cues diagnostic of the hiding event. Apes saw distinctive food being hidden in a novel location. After a retention period of 2, 10 or 50 weeks, they returned to the room in which the event took place. Upon discovering a piece of the previously hidden food on the ground, they immediately searched the location where the food was previously hidden (Figure 3), despite no food being present there. Conversely, apes that had not witnessed a hiding event did not search. The immediate behavioural response of the apes in response to diagnostic cues is consistent with the fast retrieval times observed in involuntary episodic retrieval in humans (e.g., Berntsen et al., 2013). Importantly, the apes only witnessed the event once and retrieved the memory in the absence of any task requiring goal-directed retrieval, suggesting similarities with human involuntary memories (Berntsen, 2010). Further similarities were also found in the rate of forgetting over time. In humans, forgetting often follows a logarithmic function (Rubin & Wenzel, 1996), in which information is lost rapidly at first, but then levels over time (Ebbinghaus, 1964). We observed this same result in apes (Figure 4).

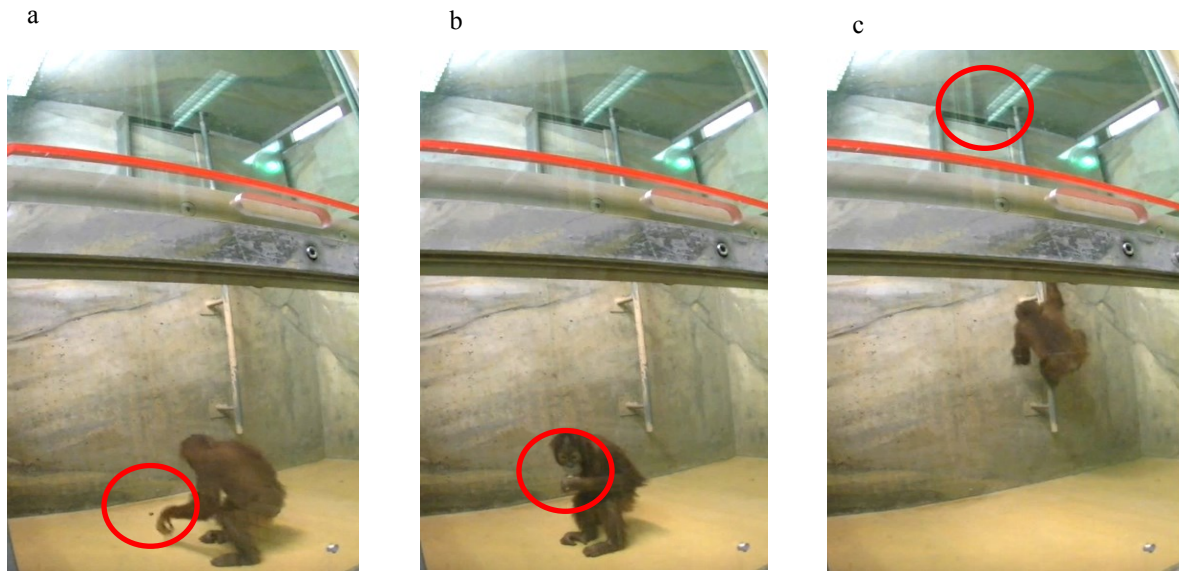


Figure 3. Still frames of an orangutan (Tanna) during a retrieval session. Tanna finds a cardamom flavoured pellet on the ground (a), she smells the pellet and eats it (b), before climbing and searching the location (indicated by the red circle) in which cardamom pellets were hidden two weeks previously (c).

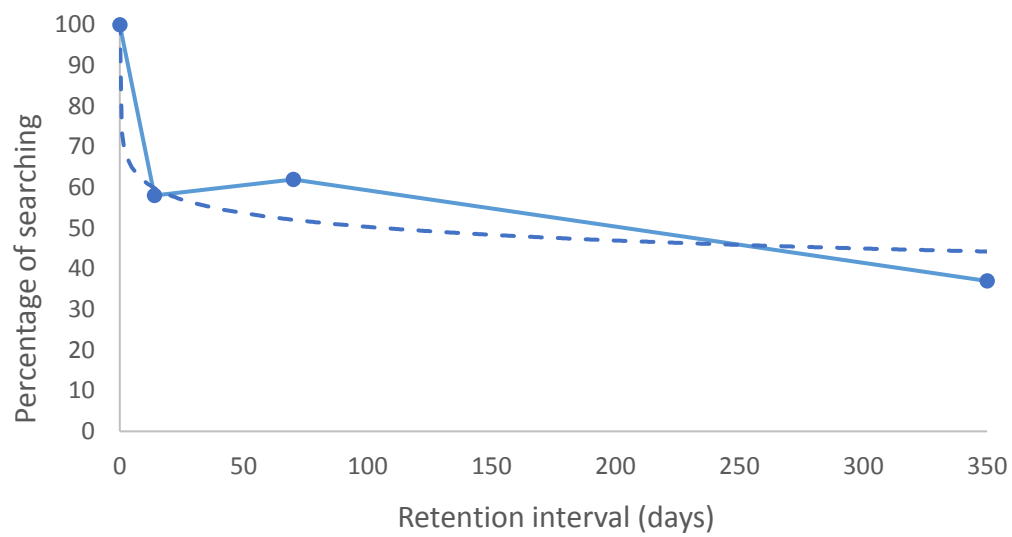


Figure 4. Percentage of searching over time. Solid circles show the retention periods (i.e., first dot shows memory after 5 minutes, the second after 2 weeks, the third after 10 weeks, the fourth after 50 weeks). Dashed line shows retention as a logarithmic function (adapted from Lewis et al., 2017b).

Conclusions

Episodic memory in animals has conventionally been investigated using Clayton and Dickinson's (1998) episodic-like paradigm. However, the extensive and varying criteria required to meet the definition of episodic-like memory has complicated progression. We, among others (e.g., Basile, 2015; Powell, Mikhalevich, Logan, & Clayton, 2017) propose that further advances will be made by investigating the similarities and differences between human and animal memory using alternative approaches. Here we have described an approach based on insights from research on involuntary memories of past events in humans.

We have shown that apes remember past events when probed by features that are diagnostic of the past event, consistent with encoding specificity and cue overload explanations of involuntary memory retrieval in humans. Although this research documents behaviour consistent with the occurrence of spontaneous event memories in apes, we acknowledge that we cannot comment on whether apes consciously recollect a past event (since they provide no verbal descriptions). However, the findings reviewed point to a behavioural reliving of a memory (a re-enactment of a past event) that is triggered in ways consistent with involuntary memories in humans. These findings seem to indicate important similarities between memories for past events in apes and humans, suggesting that the ability to spontaneously recollect past events may be shared across species.

Future research may use the present approach for research on event memory in other species. Moreover, other aspects of episodic memory, such as retrieval effort or the influence of emotion or age deserve some research attention from a comparative perspective. These aspects have received considerable research attention in the human literature, but remain largely unexplored in animals. Such comparative insights may enrich the field by mapping the mechanisms and the evolution of episodic memory in humans and other animals.

Acknowledgements and end notes

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